

THE GENUS *LIPARA* MEIGEN (DIPTERA, CHLOROPIDAE),
SYSTEMATICS, MORPHOLOGY, BEHAVIOUR, AND ECOLOGY

by

M. CHVÁLA ¹⁾, J. DOSKOČIL ¹⁾, J. H. MOOK ²⁾ & V. POKORNÝ ³⁾

ABSTRACT

Four species of the genus *Lipara*, viz.: *L. lucens*, *similis*, *rufitarsis* and *pullitarsis*, occur in Europe, where they cause galls in Common Reed (*Phragmites communis*). The specific differences of eggs, larval, and adult stages are described, and a general account is given of the life cycle, gall formation, precopulatory and ovipositional behaviour, habitat relations, and influence of parasites and predators with emphasis on the known differences between the species.

CONTENTS

1. Introduction	2
2. Systematics and morphology	2
a. Adults	2
b. Immature stages	6
Eggs	6
Larvae	6
Puparia	10
3. Life cycle and influence on the reed stems	10
a. Life cycle and gall formation	10
b. Description of the galls	10
4. Behaviour of adults	14
a. Precopulatory behaviour	14
b. Egg-laying behaviour	14
5. Ecology	16
a. Habitat relations	16
b. Parasites	21
c. Predators	24
6. Acknowledgements	24
7. References	24

¹⁾ Department of Systematic Zoology, Faculty of Natural Sciences, Charles University, Viničná 7, 128 44 Praha 2, Czechoslovakia.

²⁾ Institute of Ecological Research, Kemperbergerweg 11, Arnhem, the Netherlands.

³⁾ Institute of Scientific and Technical Information, Czechoslovak Academy of Agriculture, Slezská 7, 120 56 Praha 2, Czechoslovakia.

1. INTRODUCTION

The galls on Common Reed (*Phragmites communis* Trin.), caused by flies of the genus *Lipara*, have attracted the attention of many generations of entomologists in Europe. During more than one hundred years, after several entomologists in Vienna had collected reed galls and studied their inhabitants (Schiner 1854, Heeger 1856, Loew 1858, Giraud 1863), three species were recognized: *L. lucens*, *rufitarsis*, and *similis*.

In 1957 Ruppolt mentioned the occurrence of two types of larvae of *L. rufitarsis*, one in typical galls and the other in galls indential to those of *L. lucens*. He supposed that these might be two different species.

From 1967 to 1970, Pokorný took up the problem again in Czechoslovakia, and found that the two types of *L. rufitarsis* make distinctive galls. The differences he observed also in the life cycle and the behaviour of the larvae were such that he expected the insects to belong to two different species. He submitted the adults, bred from the galls, to Doskočil and Chvála who indeed recognized them as two different species, one being *L. rufitarsis* and the other, a previously undescribed species which they named *L. pullitarsis* (Doskočil and Chvála, 1971).

In recent years Mook studied the ecology of *Lipara lucens* in the Netherlands (Mook, 1961, 1967) and also collected data on the ecology of *L. rufitarsis* and *pullitarsis* (*L. similis* does not occur in the Netherlands). In co-operation with Miss C. G. Bruggemann he studied the behaviour of the adult of *L. lucens* (Mook and Bruggemann, 1968, 1971) and also collected data on the behaviour of the other species. These data corroborate the view that four different species are involved.

It seemed worth while to collect both the published and the unpublished data in order to give a survey of the similarities and differences in the biology of the four species. The results are presented here. The authors have each treated those aspects of the biology with which they are most familiar, and they remain responsible for the relevant section: Chvála and Doskočil for section 2, Pokorný, for section 3 and Mook, for sections 4 and 5. It should be kept in mind that the different geographical localities where the authors collected their data may have influenced their findings.

2. SYSTEMATICS AND MORPHOLOGY

a. Adults

Genus *Lipara* Meigen, 1830

Lipara Meigen, 1830: 1. Type species, *Lipara lucens* Meigen, 1830 (monobasic).

Homalura Wiedemann, 1830: 573 (nec Meigen, 1826), junior homonym. Type species, *Homalura grisea* Wiedemann, 1830 (monobasic).

? *Gymnopoda* Macquart, 1835: 503, subjective synonym. Type species, *Gymnopoda tomentosa* Macquart, 1835 (monobasic).

The genus *Lipara* Meigen belongs to the family Chloropidae, subfamily Oscinellinae, and comprises medium-sized to large blackish species, 3.3—7.3 mm, with dense pale pubescence on mesonotum. Arista thin, not pubescent, antennae broadly separated at base by a wide pollinose facial keel, very prominent in lateral aspect. Eyes rather small and finely pubescent, face very deep, almost as long as one half of the eye-height; vibrissal angles absent.

The genus nearest related to *Lipara* is *Calamoncosis* Enderlein which comprises distinctly smaller species, 2-3 mm, with equally oval head in profile, with facial "keel" only indistinctly developed. In *Lipara* the facial keel is prominent and very broad over the whole length, as far as the mouth cavity, or, if it is narrowed in the middle between the antennae, again widening out below; viewed from the side, the keel is strongly prominent above the antennae, as is the lower part of the frons, so that the head in profile is strongly prominent anteriorly.

The larvae of all *Lipara* species cause more or less distinct galls on stems of the Common Reed (*Phragmites communis* Trin.).

The genus has been recently revised by Doskočil and Chvála (1971) and as a result four Palaearctic species (viz., *lucens*, *similis*, *rufitarsis*, and *pullitarsis*) were introduced as essentially European species. Two of them, *lucens* and *similis*, have been found separately as immigrants in North America.

The four Palaearctic *Lipara* species may be keyed as follows:

- 1 Thoracic pubescence long, arranged in longitudinal stripes, producing a ridged appearance. Large or smaller species 2
- Thoracic pubescence shorter, uniformly spread, not arranged in stripes. Smaller species 3
- 2 Thoracic pubescence brassy-yellow. Large species, 5.3—7.3 mm, facial keel very broad *lucens*
- Thoracic pubescence whitish. Smaller species, 3.3—4.6 mm, facial keel narrower *similis*
- 3 Facial keel broad, with almost parallel sides, about as broad as one-half of antennal segment 3. Male genitalia with fused cerci. Length 3.3—5.0 mm *pullitarsis*
- Facial keel narrowed in the middle, widening above and below, less broad than one-third of antennal segment 3. Male genitalia with paired cerci. Length 3.5—5.3 mm *rufitarsis*

Lipara lucens Meigen, 1830

Lipara lucens Meigen, 1830, Syst. Besch. 6: 1.

Homalura grisea Wiedemann, 1830, Aussereurop. zweifl. Ins., 2: 573.

? *Gymnopoda tomentosa* Macquart, 1835, Hist. nat. Ins. Dipt., 2: 502.

Diagnosis. A conspicuously large and robust species, 5.3—7.3 mm, the largest species of the genus and family in the Palaearctic region. Thorax with long, brassy-yellow pubescence on mesonotum which is arranged in distinct longitudinal stripes, producing a ridged appearance. Antennae yellowish on basal segments, segment 3 mostly blackish. Facial keel conspicuously broad and with almost parallel sides. Legs extensively darkened. Male genitalia (Fig. 2) large, with small but rather widely separated, apically pointed cerci.

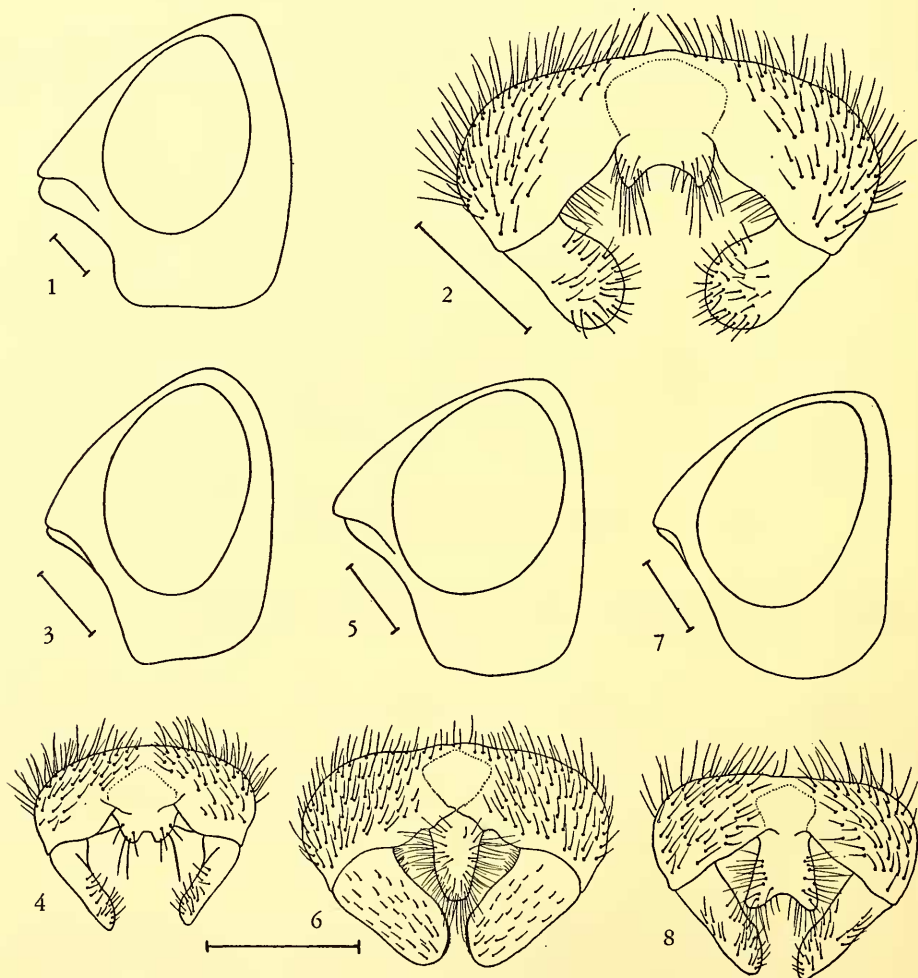
Distribution. A widely distributed and everywhere common species in Europe, ranging in the North from England through the Netherlands, Denmark, and southern Sweden, eastward as far as the northern regions of the European part of the USSR, a very common species in central and southern Europe, immigrant in North America (Connecticut).

Lipara similis Schiner, 1854

Lipara similis Schiner, 1854, Verh. zool.-bot. Ges. Wien, 4: 172.

Diagnosis. Closely related to *lucens*, having the same type of long pubescence on thoracic disc which is arranged in distinct longitudinal stripes, producing a ridged appearance. In contrast to *lucens*, the thoracic pubescence is distinctly whitish to silvery-grey; *similis* is a much smaller species, 3.3—4.6 mm. Facial keel rather broad, slightly widened above and below. Antennae and palpi yellowish. Legs mostly yellow on tibiae and tarsi, but in some specimens tarsi extensively darkened. Male genitalia (Fig. 4) small, cerci not very wide apart, small, and apically distinctly rounded.

Distribution. The species is rather common and widely distributed in Central Europe (Poland, Germany, Czechoslovakia, Austria, and Hungary), and has also been recorded from England, France, and the western regions of the European part of the USSR.



Figs. 1—8. Head in profile and male genitalia (caudal view) of *Lipara*: 1, 2, *lucens* Meig.; 3, 4, *similis* Schin.; 5, 6, *L. pullitarsis* Dosk. et Chv.; 7, 8, *L. rufitarsis* Loew. Scale = 0.3 mm

According to Sabrosky (1958), the species was intercepted in the USA (Hoboken) in *Phragmites* packing from a ship from the Netherlands. It was also mentioned for the Netherlands by Docters van Leeuwen (1957), but his description and illustration of the gall do not fit. The species has not been reared from Dutch galls (de Meijere, 1949). Dr. Th. van Leeuwen, Dr. W. J. Kabos, Dr. G. Kruseman (Amsterdam) and Dr. S. J. van Ooststroom (Leiden), who were so kind as to inform us of their experiences, also did not find the species in the Netherlands.

***Lipara pullitarsis* Doskočil et Chvála, 1971**

Lipara pullitarsis Doskočil et Chvála, 1971, Acta ent. bohemoslov., 68: 102.

Diagnosis. A smaller species, 3.3—5.0 mm, with mesonotum densely covered with mostly brassy-yellow short pubescence, not arranged in longitudinal ridges. Facial keel very broad, the narrowest part in the middle about as broad as half the width of antennal segment 3. Antennae mostly black, only basal segments sometimes very dark brown; palpi black. Legs mostly black, extreme tips of femora and extreme bases of tibiae slightly brownish; fore tarsi black, posterior four tarsi yellowish-brown on basal segments, apical segments extensively darkened. Male genitalia (Fig. 6) rather large, with broad parameres and entirely fused long cerci. The Central European and southern Scandinavian populations have extremely darkened antennae and legs, but we have seen paler specimens from the Netherlands that superficially resemble *rufitarsis*, differing from the latter by a much broader facial keel and quite distinct male genitalia.

Distribution. This species has long been confused with *rufitarsis*, and it is highly probable that many records on the distribution of *rufitarsis* refer, in fact, to *pullitarsis*. The species was described very recently from Czechoslovakia but we have also seen documentary material from the Netherlands, Denmark, and Sweden.

***Lipara rufitarsis* Loew, 1858**

Lipara rufitarsis Loew, 1858, Wien. Ent. Monatschr., 2: 57.

Diagnosis. A smaller species, 3.5—5.3 mm, resembling *pullitarsis* in having the same type of pubescence on thoracic disc; the hairs are short and not arranged in longitudinal ridges but, in contrast to *pullitarsis*, the pubescence is distinctly silvery-grey and the hairs on the hind part of mesonotum and on the scutellum are distinctly longer. Facial keel is much narrower than in *pullitarsis*, widening above and below, the narrowest part in the middle being hardly as broad as one-third the width of antennal segment 3. Antennae reddish-brown except for outer side of segment 3 and arista which are extensively darkened or almost black; palpi black. Femora and tibiae predominantly black, the apical tips of femora, both rather broader tips of tibiae and whole tarsi yellowish- to reddish-brown. Wings with cubital and discal veins almost straight, not curved as in *pullitarsis*. Male genitalia (Fig. 8) rather large, with narrower parameres, long cerci apically distinctly separated.

Distribution. *L. rufitarsis* is recorded in the literature as a common species throughout Europe, but at least some of these records must concern *pullitarsis*. We have seen the documentary material from the Netherlands, Czechoslovakia, Austria, and Italy, and

according to Dr. Hackman (letter of 24.8.1971), the material from southwestern Finland also belongs to *rufitarsis*. On the other hand, having revised in Copenhagen and Lund all of the accessible *rufitarsis* material from Denmark and southern Sweden, one of the authors (Chvála) comes to the conclusion that all of it belongs to *pullitarsis*.

b. Immature stages

There are few older data on immature stages of *Lipara*; a summary of all the records up to 1950 is given by Hennig (1952). He found only four records of larva and puparium of *lucens* in the literature, but the record of larva by Vimmer (1925), must, in fact, refer to *rufitarsis* judging from the Czech description and figures. Ruppolt (1957) described eggs and larval stages of *lucens*. The most complete treatment of the morphology of immature stages of *lucens* is by Waitzbauer (1969). No other records are available.

Most of the eggs, larvae, and puparia used for the study discussed in this section, belong to material collected and bred by J. H. Mook and V. Pokorný.

Eggs

The eggs of the four Palaearctic *Lipara* species are very distinctive. In general, they may easily be separated into two different groups, viz., (1) the *lucens* type and (2) the *rufitarsis* type. The former type (*lucens* and *similis*) is characteristically rather broader, more oval, and light yellow in colour. The differences between the eggs of *lucens* (Plate 2b) and *similis* (Plate 2d) are very slight; the egg of *similis* is almost as long and as wide as that of *lucens*, but the latter has more distinct sculpture, consisting of rather deep longitudinal furrows (Plate 2a). The measurements of the eggs of these two species are as follows: *lucens*: (N = 40) length 1.37—1.69 mm (M = 1.57 mm), width 0.25—0.36 mm (M = 0.32 mm); *similis*: (N = 20) length 1.35—1.46 mm (M = 1.42 mm), width 0.23—0.32 mm (M = 0.27 mm). The ratio of length to width is about 5 : 1 in both *lucens* and *similis*.

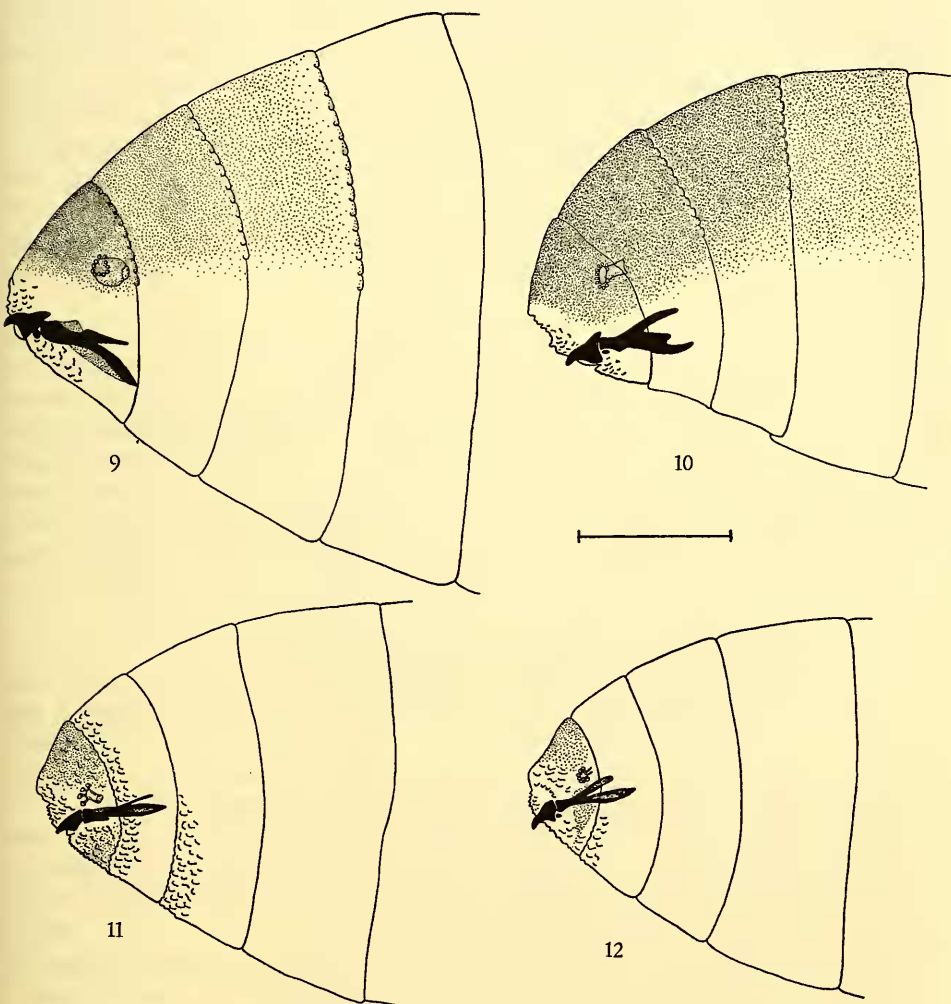
The second type of egg (*rufitarsis* and *pullitarsis*) is characteristically long and narrow, and distinctly blackish in colour. The egg of *pullitarsis* (Plate 3b) is distinctly narrower, slightly shorter, rather circular in cross-section, and the longitudinal furrows (Plate 3a) are quite distinct. The eggs of *rufitarsis* (Plate 3d) is less slender but slightly longer, somewhat triangular in cross-section (rounded above, flattened below), and the longitudinal furrows are less numerous and barely visible; the whole egg is therefore rather smooth. The measurements of these two eggs are: *pullitarsis*: (N = 30) length 1.13—1.26 mm (M = 1.21 mm), width 0.07—0.11 mm (M = 0.09 mm); *rufitarsis*: (N = 40) length 1.39—1.53 mm (M = 1.50 mm), width 0.15—0.20 mm (M = 0.18 mm). The ratio of length to width in *rufitarsis* is 8 : 1, in *pullitarsis* 13 : 1.

Larvae

Larvae are elongate, light yellowish, with one or both tips more or less sclerotized; the length of mature larvae varies from 5.5 to 12 mm; all measurements were taken from larvae collected in the winter or early spring. The whole body is rather smooth, integument exclusively with regularly spaced flower-like not sclerotized papillae and sometimes with striae, especially on anterior segments. The sclerotization of anterior and posterior segments, including the number of buds on anterior spiracle, seem to be

the best specific characters. Posterior spiracle consists of three simple radiating slits, interstigmatal processes are branched (? absent in *rufitarsis*).

The mature larva of *lucens* (Plate 6a) is conspicuously large and stout, 8—12 mm in length and 2—3 mm in width. Only anterior segments dorsally sclerotized (Fig. 9), more heavily on segment 1 as far as the anterior spiracle, a slight sclerotization continues over anterior spiracle on dorsum of segment 2 and anterior half of segment 3. Segment 1 sometimes also slightly sclerotized ventrally. Posterior margin of anterior three segments on dorsum with small sclerotized papillae in a row; on venter also present but hardly visible (not sclerotized). Anterior spiracle (Fig. 13) with 11 to 12 (exceptionally up to 14) buds, their number not constant on each side; the usual combinations are 11—11, 11—12, or 12—12, in rare cases, 12—13 or 12—14.



Figs. 9—12. Four anterior segments of mature larva of *Lipara* (lateral view). 9, *L. lucens* Meig.; 10, *L. similis* Schin.; 11, *L. pullitarsis* Dosk. et Chv., 12, *L. rufitarsis* Loew. Scale = 1 mm

The mature larva of *similis* (Plate 6b) generally is smaller and especially more slender, 5.5—10 mm in length and 1—2 mm in width; it is the only species of the genus with distinct sclerotization of both tips. Segment 1 (Fig. 10) heavily sclerotized dorsally, except for a narrow anterior strip, segments 2 and 3 heavily sclerotized dorsally, almost blackish, as is segment 1. Segment 4 dorsally with a slight sclerotization, venter of four anterior segments pale, membranous. Segments 5 to 10 membranous, segment 11 slightly sclerotized dorsally and ventrally, almost membranous laterally. Segment 12 heavily sclerotized throughout, having the same blackish colour as anterior three segments dorsally. Posterior margins of segments 2, 3, and 10 dorsally with a row of slightly sclerotized papillae, these membranous only on venter. Anterior spiracle (Fig. 14) with 9 to 11 buds with usual combinations 9—9, 9—11, 10—11, 11—11, or 9—10.

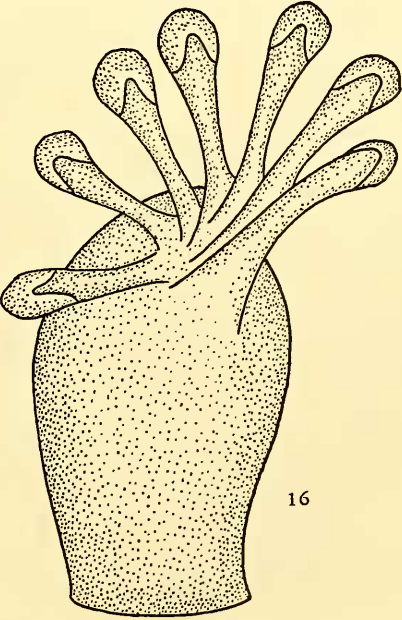
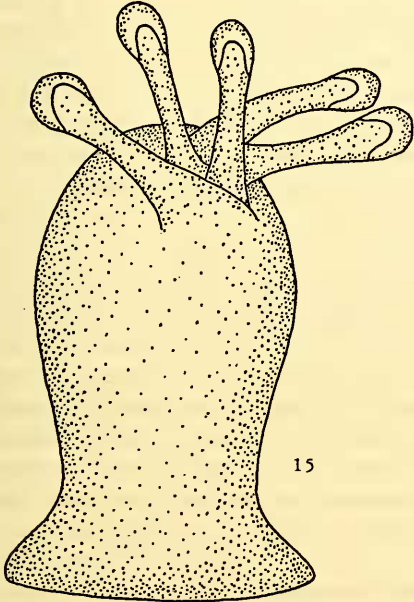
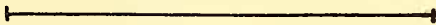
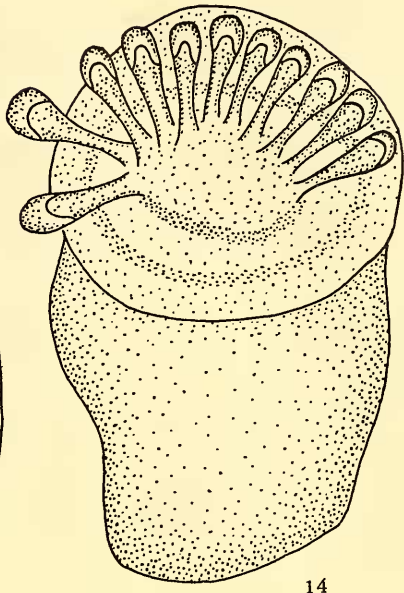
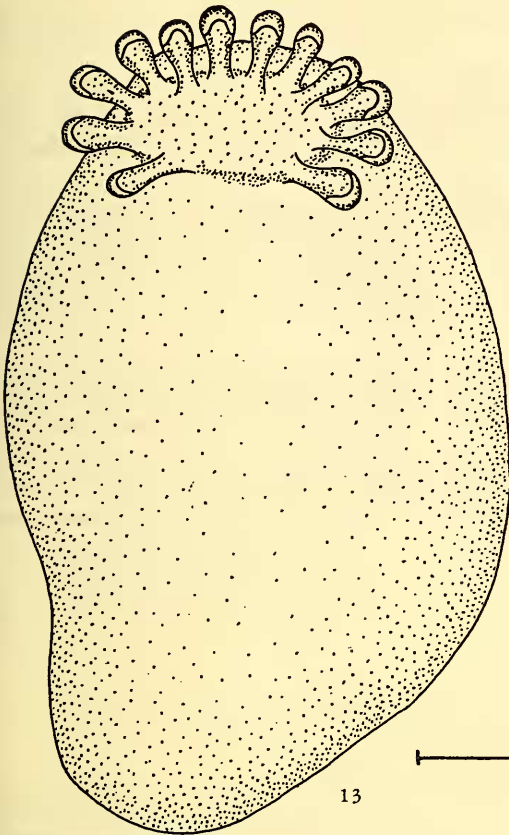
The mature larva of *pullitarsis* (Plate 6c) is 6.5—9 mm long and 1.5—2 mm wide, with sclerotization on segment 1 similar to that in *rufitarsis*. Dorsum of segment 1 (Fig. 11) more or less heavily sclerotized, lateral area almost membranous, and venter evenly and slightly sclerotized, without any distinct pattern. Slight sclerotization also visible on the anterior ridge. No rows of membranous papillae have been found on posterior margins, but distinct papillae are visible on anterior ridge and among the striation on segment 1 ventrally; this segment distinctly striated both ventrally and dorsally, segment 2 on anterior half dorsally and ventrally, segment 3 on anterior half ventrally only. Otherwise the integument is smooth, except for regularly spaced, small, flower-like papillae. Anterior spiracle (Fig. 15) with 4 to 5 buds, the number on each side often differing.

The mature larva of *rufitarsis* (Plate 6d) has in general much in common with *pullitarsis*; it is rather smaller, 6—8.5 mm long and 1.5—2.5 mm wide, more or less sclerotized only on segment 1. The dorsal sclerotization (Fig. 12) is not very distinct (light brown in colour), almost interrupted laterally near anterior spiracle and again more distinct on a triangular patch ventrally. Papillae on posterior margins always membranous and therefore inconspicuous. Whole of segment 1 distinctly striated except for the anterior ridge, which bears very small, not sclerotized papillae. Segment 2 with fine striae on anterior half ventrally, otherwise segments smooth. Anterior spiracle (Fig. 16) with 6 to 9 buds in combinations 7—8, 8—9, 7—7, 6—7, or 6—6.

The mature *Lipara* larvae may be keyed as follows:

- 1 Larva heavily sclerotized (blackish-brown in colour) on both tips, anteriorly on 4, posteriorly on 2 segments. Anterior spiracle with 9 to 11 buds. Larva about 8 mm long *similis*
- Larva less heavily sclerotized (brownish in colour), only anteriorly, at most on the three anterior segments. Posterior segments pale, membranous 2
- 2 Three anterior segments slightly sclerotized on dorsum. All thoracic segments with a row of heavily sclerotized papillae on posterior margin, segment 1 without a ridge on anterior margin. Anterior spiracle with 11 to 12 (or rarely up to 14) buds. Larva about 10 mm long and very stout *lucens*
- Only segment 1 slightly sclerotized. Sclerotized papillae on posterior margins of thoracic segments absent, segment 1 with a distinct ridge on anterior margin.

Fig. 13—16. Anterior spiracle of mature larva of *Lipara*. 13, *L. lucens* Meig.; 14, *L. similis* Schin.; 15, *L. pullitarsis* Dosk. et Chv.; 16, *L. rufitarsis* Loew. Scale = 0.1 mm



- Anterior spiracle with at most 9 buds. Larvae generally smaller, about 8 mm long, and slender 3
- 3 Anterior spiracle with 6 to 9 buds. Segment 1 usually slightly sclerotized, also ventrally, distinctly striated on the whole surface, except the smooth anterior ridge; segment 2 with slight striae on anterior half ventrally; segment 3 smooth, without striae *rufitarsis*
- Anterior spiracle with 4 to 5 buds. Segment 1 usually membranous beneath, at most quite indistinctly sclerotized, but with distinct striae throughout, also on anterior ridge; segment 2 with striae on anterior half both ventrally and dorsally; segment 3 with striae on anterior half ventrally *pullitarsis*

Puparia

The puparia are brown to reddish-brown, with the same specific characters as in mature larvae, i.e. of the same size, different colour of tips, and the same number of buds on the anterior spiracle. *L. lucens* has a large and stout puparium, 8 to 12 mm long, the anterior two segments distinctly darkened dorsally, anterior spiracle with 11 to 14 buds; puparium of *similis* slightly smaller on average, distinctly blackish over three anterior and two posterior segments, anterior spiracle with 9 to 11 buds; *rufitarsis* and *pullitarsis* have smaller puparia, about 6 to 9 mm long, slightly darkened on segment 1 only, anterior spiracle with 6 to 9 buds in *rufitarsis* and 4 to 5 buds in *pullitarsis*.

3. LIFE CYCLE AND INFLUENCE ON THE REED STEMS

a. Life cycle and gall formation

By their action in the larval stage, all four *Lipara* species induce the formation of a terminal gall on the infested shoot, thus altering the length of the stem, the number and dimensions of internodes and the formation of a panicle. Each gall is ultimately inhabited by a single larva, even when shoots are infected by more than one egg.

The formation of the gall is principally the same in all four species, and is closely related to the behaviour of the larvae. The egg-laying behaviour of the fly is described in section 4. Several days after the eggs are laid the larvae hatch. In *L. lucens* the larvae hatch after about 9 days. Hatching takes place virtually only during the night. This is probably important for survival, because in order to escape drying out the larvae require a very high humidity (Ruppolt, 1957, Mook, 1967). The young larva crawls upward on the surface of the shoot until it reaches the top part, and then crawls under the edge of a leaf sheath into the roll of young leaves. There it feeds on the young leaf parenchyma and bores downward toward the growing point. Just above this point it continues to feed on the newly-formed leaves. Here the larva molts twice. The growing point is affected by the feeding of the larva and probably also by its metabolic products. Internodes formed subsequently remain shorter than the internodes of a healthy stem.

The shortening of the internodes leads to the formation of the terminal gall in the stem. The gall itself is formed (except in the case of *L. lucens*) by the leaves growing from the agglomerated nodes. The leaf-sheaths do not have sufficient room to grow parallel with the stem axis and are pushed off at an angle to it; in this way the typical cigar- or spike-like inflation develops.

Up to this point the life cycle is basically the same for all the four species. The

differences become apparent at a later stage, and therefore the rest of the life cycle will be described for each species separately.

During July or August the larva of *L. lucens* (Plate 6a) bites through the growing point and lives in the shortened internodes where it feeds on the soft parenchyma filling these internodes. In due time it gnaws a chamber passing into the 6th to 8th internode from above. At the end of the summer and in the beginning of the autumn the larva turns 180° in the chamber, so that its head is pointing upward. This turn is very important (and takes place in the other species, too), because it enables the adult to leave the gall. After turning, the larva shifts its position 2 to 3 cm higher, living without nutrition approximately 1 to 2 cm under the remnants of the growing point; at that time it is 8—12 mm long, thick, and ivory white. In this position it also hibernates and pupates in the spring. In Czechoslovakia and in the Netherlands, depending on the climatic conditions, the adults emerge as the second *Lipara* species at the end of May or beginning of June (Fig. 17).

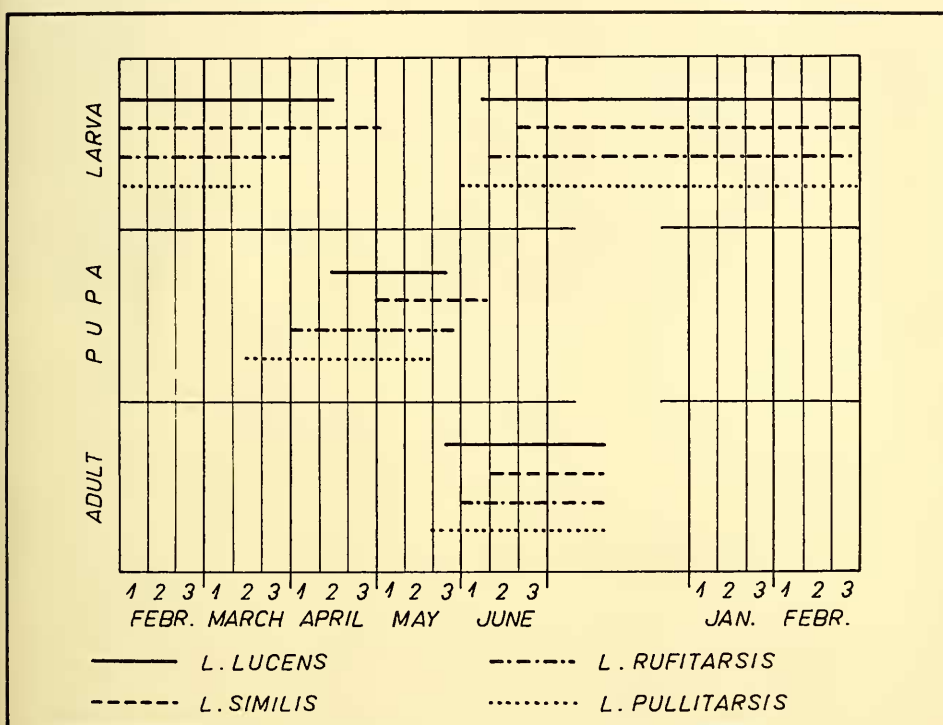


Fig. 17. Life cycle of *Lipara* species in Czechoslovakia

The growing point of the reed is also perforated by the larva of *L. rufitarsis* (Plate 6d), but in this species the chamber reaches only to the 3rd or 4th (shortened) internode from the top. The walls of the shortened internodes are not thickened and their width is the same as that of the adjacent not shortened ones. Once arrived below the growing point the larva feeds until some time around August, after which it turns and rests until spring, when it pupates. At that time it is 6—8.5 cm long, slightly yellowish, and more flattened than the larvae of the other species. The adult emerges as the third *Lipara* species at the beginning of June.

These two species are characterized by a common behaviour pattern viz., biting through the growing point and life in the chamber in the shortened internodes. The other two species leave the growing point intact, living throughout their whole lifespan between the leaves above this.

In the beginning, the larva of *L. pullitarsis* (Plate 6c) feeds on young rolled leaves in which it "chops" its chamber. Later on, when the panicle is beginning to be formed, it feeds on this rudiment often completely destroying the panicle. Sometimes, probably when infestation occurs later, a panicle large enough to survive is formed in the gall, only to have the larva gnaw through it, too, to maintain its chamber. Such panicles never develop fully. Before turning, the larva usually reaches the growing point, but after having turned, it shifts itself 3 to 5 cm above the growing point and hibernates there. At that time it is 6.5—9 mm long and white. In the spring, as soon as the days become warmer, the larva pupates as the first of the *Lipara* species and the adults emerge also as the first, in the second half of May.

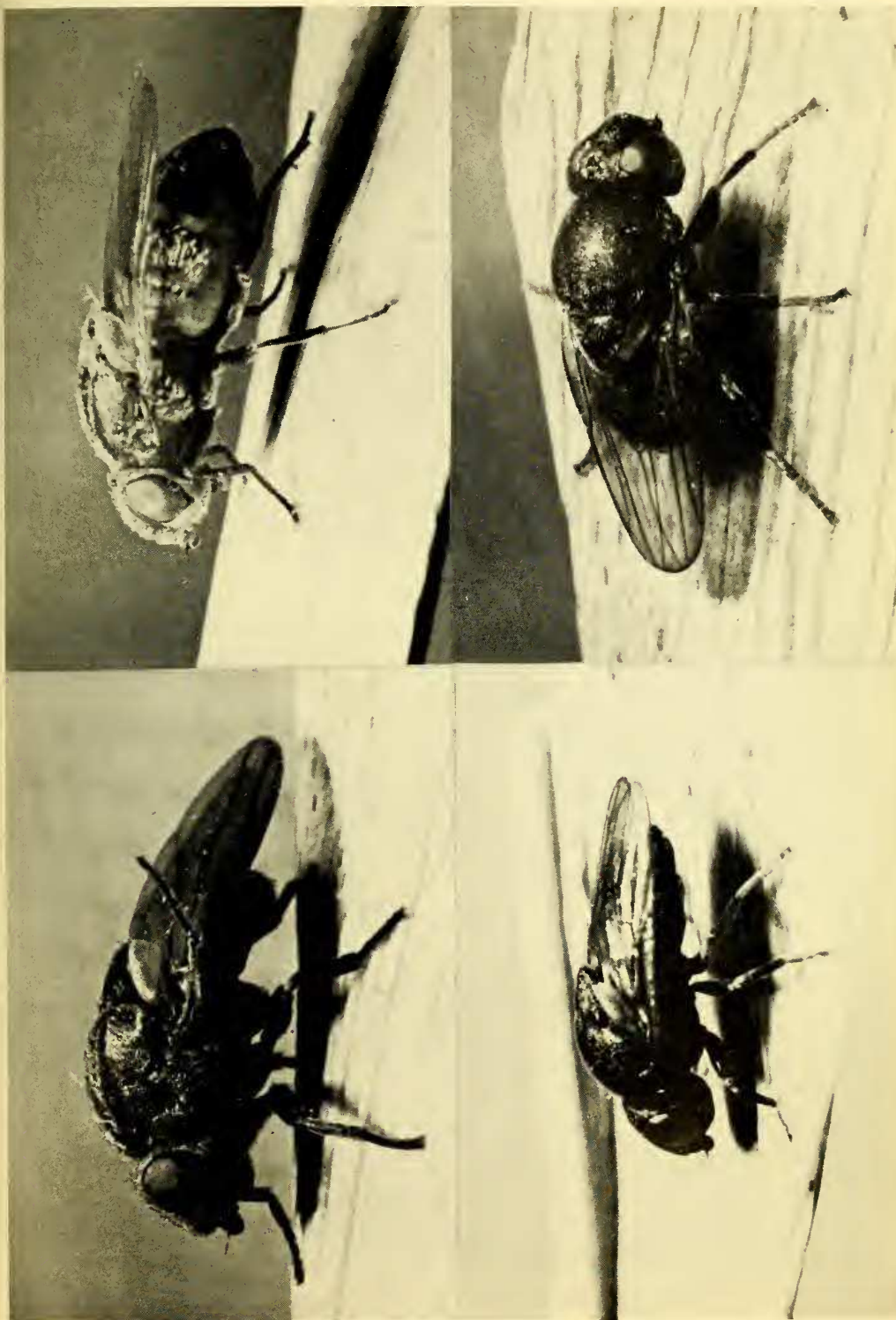
Similarly, the larva of *L. similis* (Plate 6b) lives in the tube of leaf sheaths. In the beginning it feeds on the rolled leaves, which later becomes completely severed from the growing point, so that they can be pulled out by the tips. The space between the leaves is relatively narrow and the adult larva fills it completely. As soon as the panicle begins to develop the larva starts to feed on the rudiments, thus destroying the panicle completely. Even in the narrow cleft in the tube the larva turns and shifts itself upward. During the winter and early spring, the two sheaths become hard, thus protecting the hibernating larva, which at that time lies 5 to 7 cm above the remnants of the growing point. In this period it reaches a length of 5.5 to 10 mm, and is slim, milky white, and glossy, with both ends black. In the same position, the larva pupates in spring as the last of the *Lipara* species. The adults emerge, also as the last, in the middle of June.

b. Description of the galls

The number of shortened internodes is more or less characteristic for the species and thus also for the shape of the gall (Fig. 18 and Plate 4). The most massive and prominent galls result from the influence of the larva of *L. lucens* (Plate 5a), and this corresponds with the greatest number of shortened internodes, usually 10—13. The shortened internodes are 2 to 3 times wider than the adjacent normal ones, and their walls are thickened and strongly lignified (Plate 4a). All of the 6 to 8 uppermost shortened internodes are brownish and covered with a continuous hairy layer. The agglomerated nodes are also provided with a wreath of hairs, and the leaves growing from them have short broad sheaths and weaker short blades. The highest leaves are relatively broad and short, again covered with a continuous hairy layer; these leaves do not differentiate into sheath and blade.

Due to the activity of the larvae of *L. rufitarsis* or *L. pullitarsis*, only 5 to 6 internodia are manifestly shortened (Plate 4c). The galls (Plate 5c, d) in these two species are usually similar, and can only be conclusively differentiated by a longitudinal section through the gall. The galls are medium-sized to large, the *pullitarsis* galls being usually larger, since *pullitarsis* occurs on wider shoots. This is why its galls are sometimes larger than those of *lucens*. But if the galls of *lucens* and *pullitarsis* appear simultaneously on equally wide shoots, those of *lucens* are always larger (Fig. 20).

The stem infested by *L. similis* has the smallest number of shortened internodes, i.e.



M. CHVÁLA, J. DOSKOČIL, J. H. MOOK & V. POKORNÝ : *The genus Lipara*

c Plate 1. Adults of *Lipara*. a, *L. lucens* Meig.; b, *L. similis* Schin.; c, *L. pullitarsis* Dosk. et Chv.; d, *L. vulfarsis* Loew (Phot. V. Pokorný).

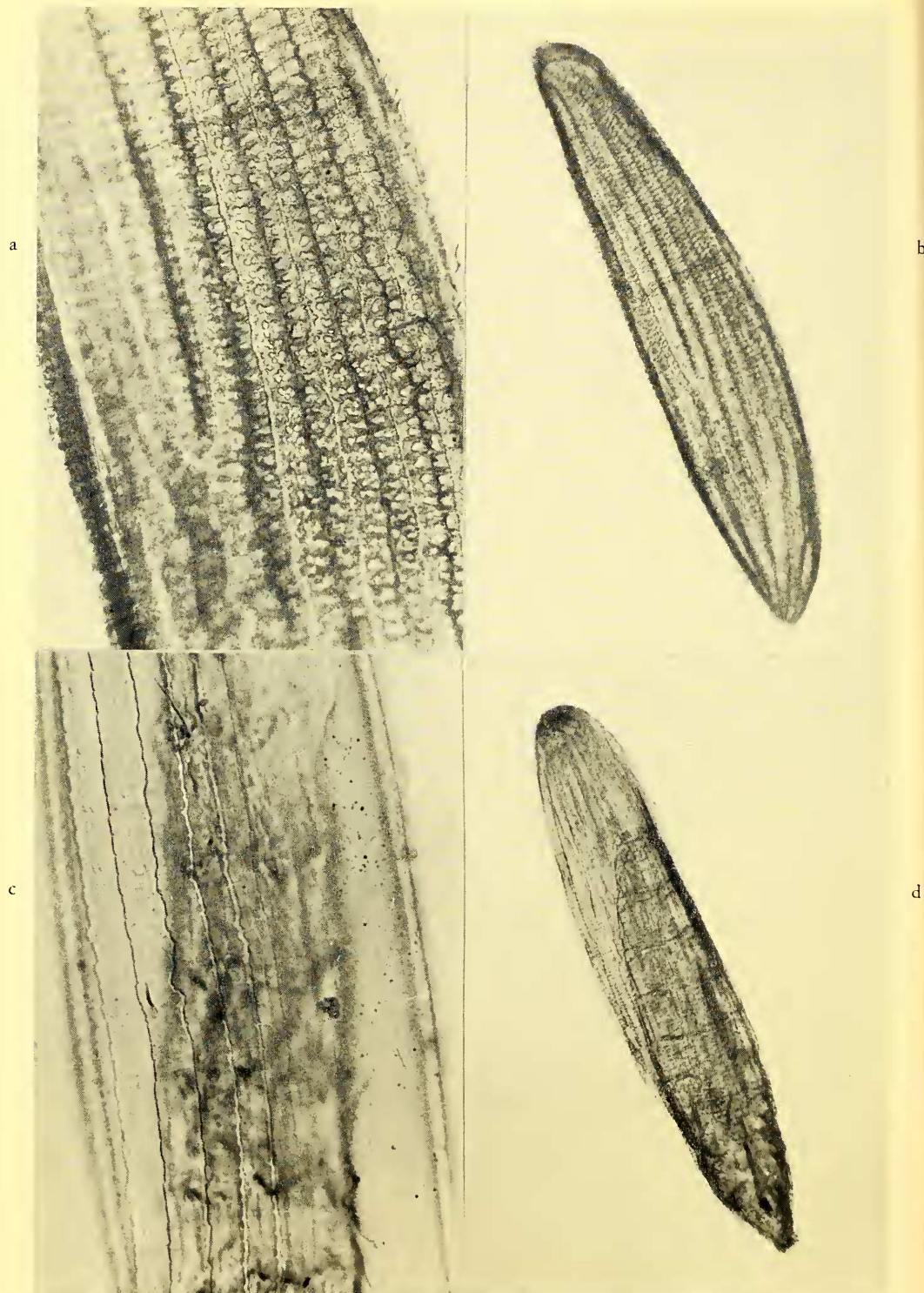


Plate 2. *Lipara* eggs with detail. a, b, *L. lucens*; c, d, *L. similis* Egg: $\times 70$, detail: $\times 160$ (Phot. J. Chalupský)

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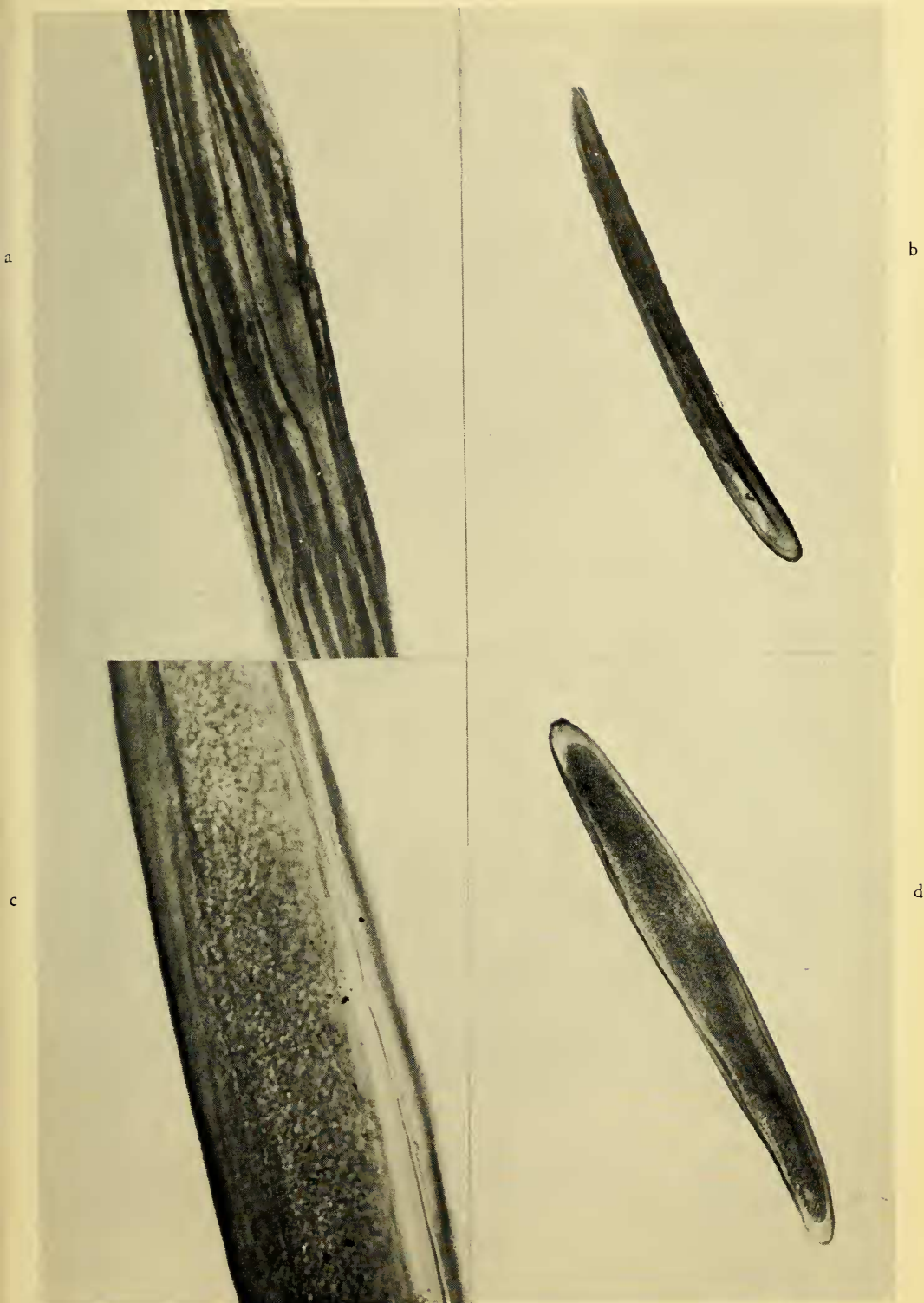


Plate 3. *Lipara* eggs with detail. a ,b, *L. pullitarsis*; c, d, *L. rufitarsis*. Egg: $\times 70$, detail $\times 160$
(Phot. J. Chalupský)

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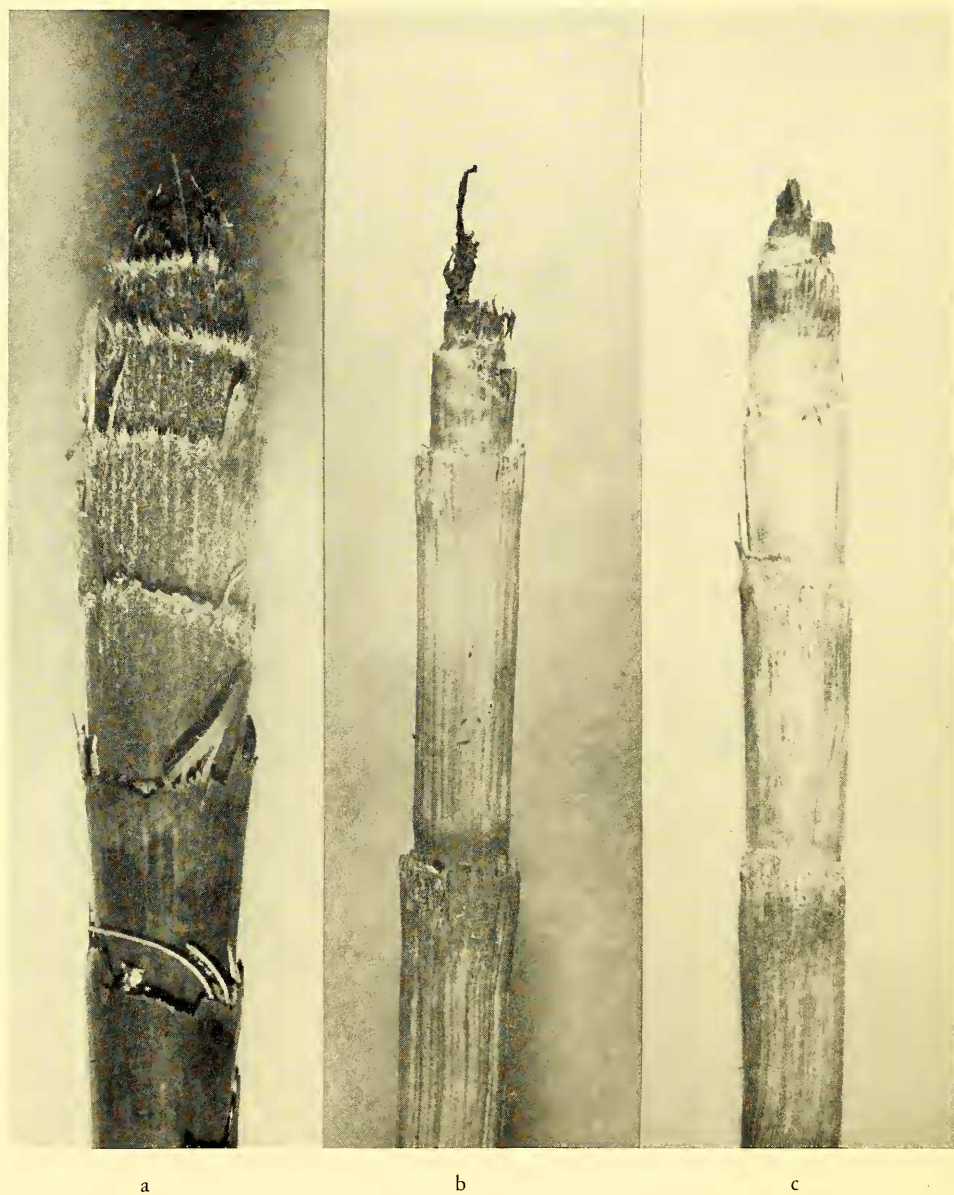


Plate 4. The highest internodes of reed stems with a gall of *Lipara*. a, *L. lucens*; b, *L. similis*; c, *L. pullitarsis* (Phot. V. Pokorný)



Plate 5. Galls typical of the individual species of *Lipara*. a, *L. lucens*; b, *L. similis*; c, *L. pullitarsis*; d, *L. rufitarsis*. The size relations are maintained (Phot. V. Pokorný)

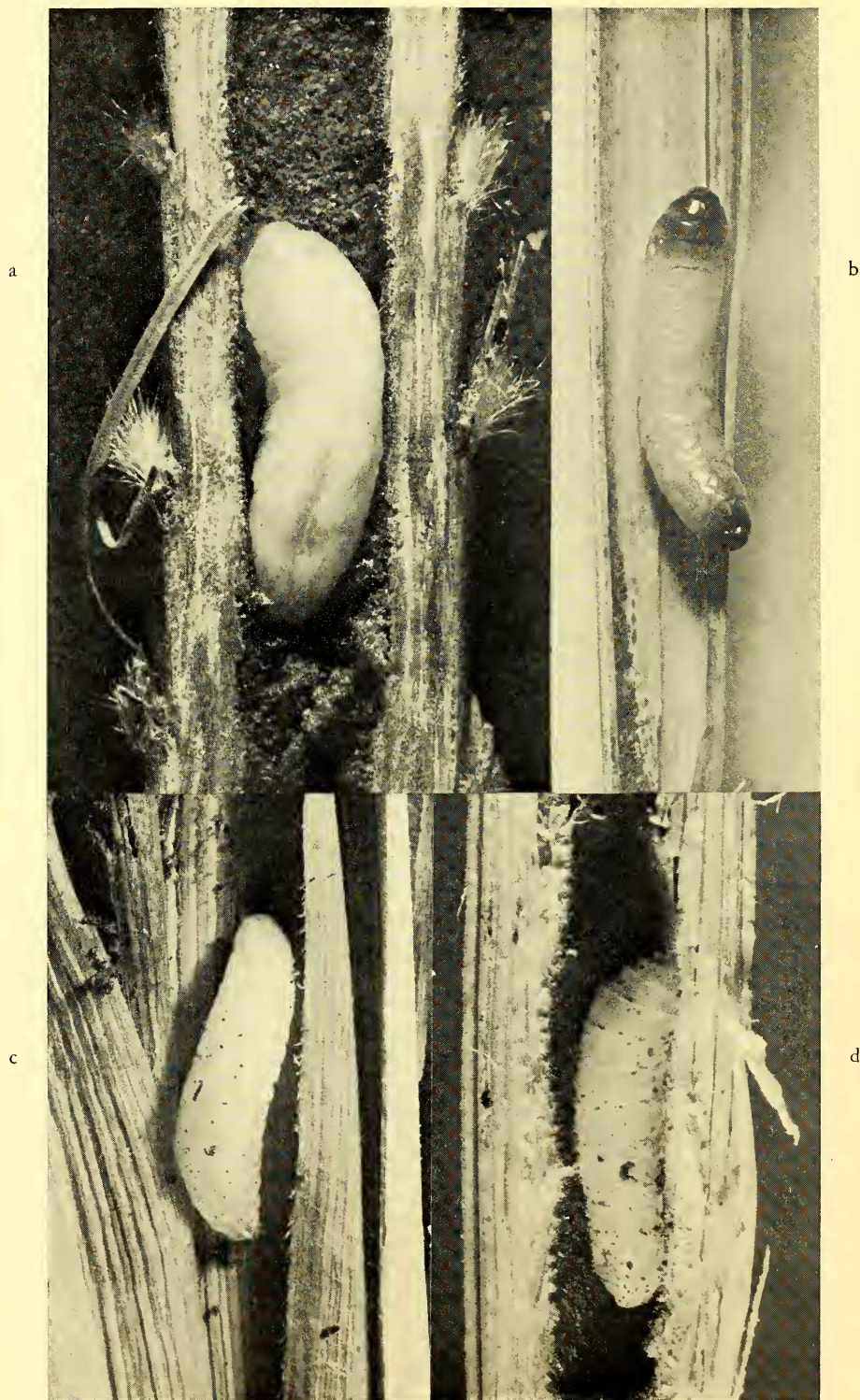


Plate 6. Larva of *Lipara*. a, *L. lucens*; b, *L. similis*; c, *L. pullitarsis*; d, *L. rufitarsis* (Phot. V. Pokorný)

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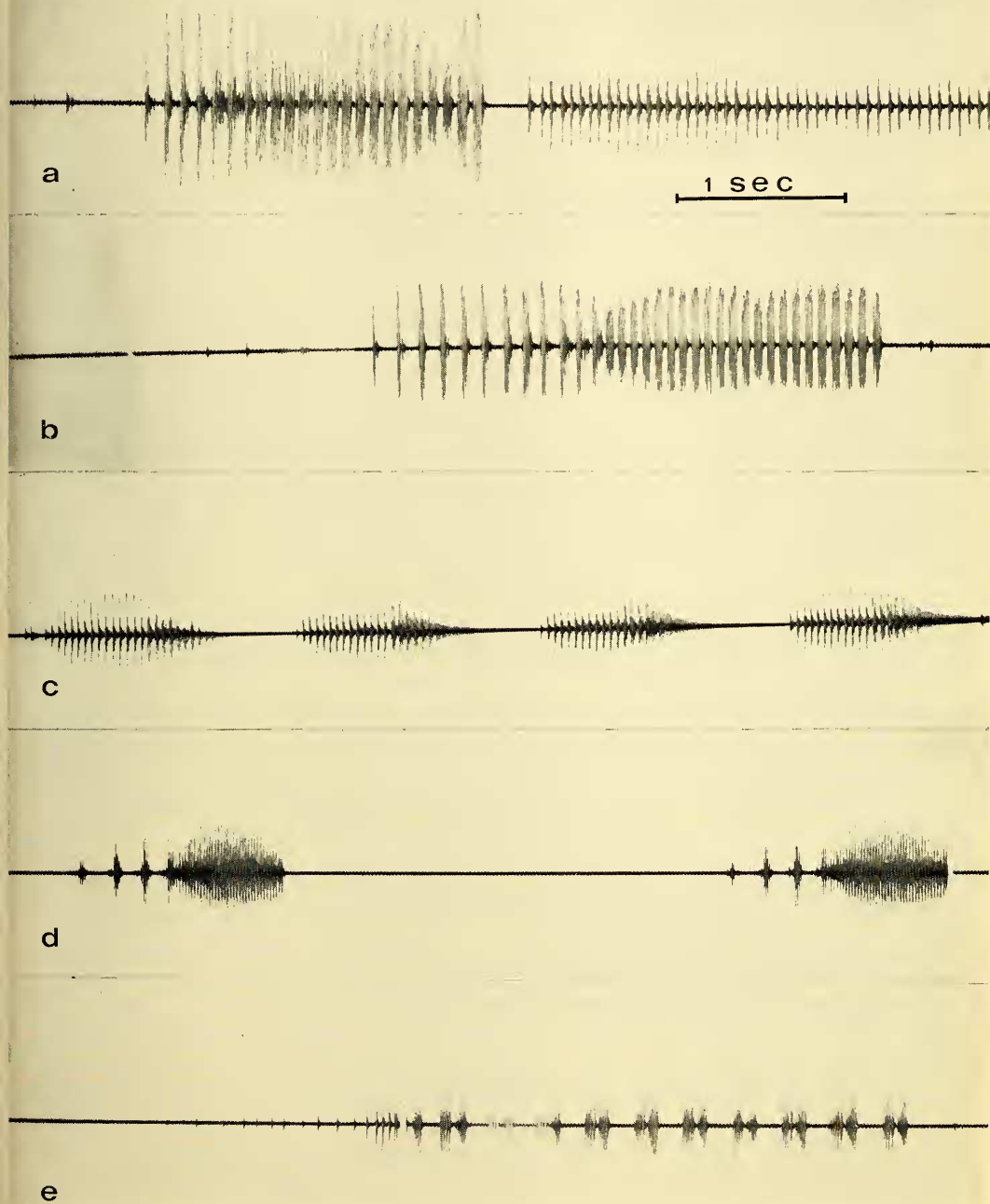


Plate 7. Signals of *Lipara* species registered with an UV recorder. a, signal of male *L. lucens* with part of answering signal of female; b-e signals of males of different species: b, *L. lucens*; c, *L. similis*; d, *L. pullitarsis*; e, *L. rufitarsis*

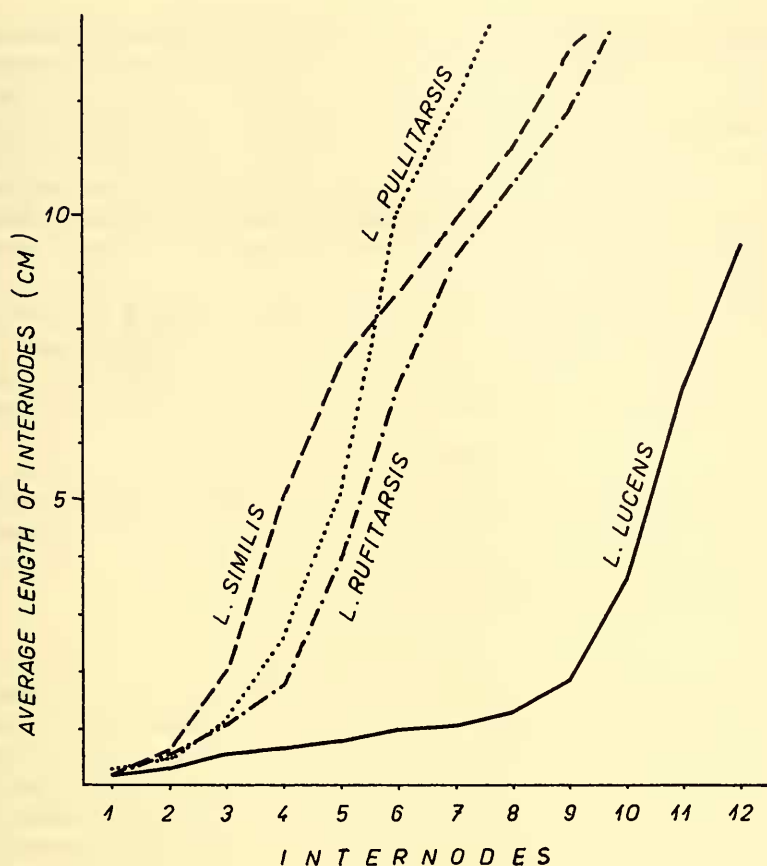


Fig. 18. Length of the highest internodes (counted from above) of reed stems attacked by larvae of *Lipara* species. (average of 30 stems per species)

3 to 4. This is why the gall is the smallest and least noticeable (Plate 5b). Due to this small number of shortened internodes and also to the fact that the shortened internodes are narrower than the adjacent normal ones but rather telescopic (Plate 4b), the sheaths have enough room and embrace the stem closely. The gall itself is formed only by the leaf sheaths growing from the two highest visible nodes which form an approximately 9 cm long tube concealing the remnants of the rolled leaves, the larva and the remainders of the panicle and the growing point. This is why the gall is not inflated and resembles the top of a sterile shoot, from which it differs only by the fact that the sheaths of the two uppermost leaves covering the gall are almost equally long.

By summarizing these descriptions we arrive to the following key to the galls:

- 1 There is a terminal inflation on the stem: a cigar- or spike-shaped gall . . . 2
- There is no terminal inflation of the stem, it looks like the top of sterile shoot.
In the tube formed by the leaf sheaths growing from the two highest visible nodes there is a slim, milky white, glossy larva with both ends black (or brown pupa with both ends black) *similis*
- 2 In a longitudinal section through the gall a chamber cutting through the young rolled

leaves can be seen. In the chamber there is a big white larva (or brown pupa). The chamber never passes through the growing point to the shortened internodes . . .

- *pullitarsis*
- The chamber passing through the rest of the growing point in order to reach the shortened internodes. Its inner walls black 3
- 3 Walls of the shortened internodes thickened, their width two or three times that of adjacent not shortened ones. The chamber passing through 6 to 9 shortened internodes, containing a big, thick, ivory white larva (or a brown pupa). The shortened internodes brown *lucens*
- Walls of shortened internodes neither thickened nor brown, their width equal to that of the adjacent not shortened ones. The chamber passing through 2 tot 4 shortened internodes only and containing a big, yellowish, and somewhat dorsoventrally flattened larva (or brown pupa) *rufitarsis*

4. BEHAVIOUR OF ADULTS

The discussion of behaviour and ecology will be somewhat one-sided, because *Lipara lucens* is by far the best known species of the four and the outline of its biology will therefore be the largest. The fragmentary information concerning the biology of the other species will be compared with that of *lucens*.

a. Precopulatory behaviour

The adults of *Lipara lucens* force themselves upward between the leaf sheaths and emerge from tip of the gall during the early morning hours. In this process an important role is played by the ptilinum, a large sac of the head, which can be expanded, so pushing aside any obstacle in front of the head. It is also useful for bursting the puparium, and in other species of higher flies, for forcing a way up through the soil (Oldroyd, 1964). In the hardening process after emergence, the ptilinum is retracted inside the head.

The flies emerge over a period of two or three weeks in the end of May or the beginning of June. Our observations do not indicate that the female flies emerge a few days before the males, as is stated by Waitzbauer (1969).

The female flies are probably very sedentary before copulation, but detailed observations on the behaviour in the field are not yet available. In laboratory experiments, where the flies are observed in small cages provided with some old reed stems, the females remain in the same place for a long time unless the temperature becomes high (above about 25° C), when they become restless. The males move about much more, and it is often obvious that they are in search of a female. They fly from reed stem to reed stem, on each stem giving a signal by vibrating. A virgin female fly sitting on the same substrate as the male perceives this signal as a vibration of the substrate and immediately answer by vibrating in its turn (Plate 7a). This in turn induces in the male increased searching on the reed stem. It starts to walk over the stem, stops after a few seconds to give a signal again, and when this is answered, begins to walk again. In this way the male finally finds the female, and copulation often takes place without obvious further display.

When a male gives its signal on a stem and does not receive an answer, it soon leaves the stem and flies to another. Therefore the function of this behaviour seems obvious. This procedure requires much less time than the male would need for searching the whole reed stem.

The signals of both the male and the female fly cannot normally be heard by the human ear, but the male's signal is perceived when seated on a reverberating substrate. Both signals can be made audible by placing a crystal gramophone pick-up element in contact with the substrate, for instance a reed stem, and by connecting this element to a tape recorder. The tape recordings can then be converted to visual signals with the help of an oscilloscope or an UV recorder (Plate 7).

This description is based primarily on observations of *L. lucens* (Mook and Bruggemann, 1968, 1971), but behaviour of other species is known to be similar. Important differences between species were found in the signals of the males, characteristic examples of which are given in Plate 7b-d. The main pitch of these sounds is about the same (a few hundred Hz.), but there are wide differences in the rhythm making it easy to recognize the different species by their signals. There are no great differences between the signals of the females. They all have a pattern similar to the one shown in Plate 7a; only the duration varies, that of *L. pullitarsis* being characteristically short (one or two seconds) while that of the other species is usually longer (up to over 10 seconds). No differences were found between the signals of flies collected in Czechoslovakia and the Netherlands.

Because such marked differences were found between the signals of the males, an experiment was set up in order to investigate whether these differences play a role in reproductive isolation. In this experiment, sounds of three species of *Lipara* and two species of *Haplegis* (small Chloropid flies, the larvae of which occur asinquilines in *Lipara* galls) were played back to females of the three *Lipara* species. The female flies rested on a strip of paper in contact with a small loudspeaker (output 0.5 watt). The tape gave each of the signals ten times in a random sequence, with a 30 second interval between signals. The tape was played back twice to each of five females of the three different species, so that each female was subjected to each signal twenty times, and their response was observed with a binocular microscope. The number of responses (Table I) was high only for the own species, which makes it probable that the signals do indeed play a role in reproductive isolation.

Table I. Reactions of 5 females of 3 *Lipara* species to 20 male signals of 5 different Chloropidae

♂ signal	Reactions of ♀														
	<i>lucens</i>					<i>pullitarsis</i>					<i>rufitarsis</i>				
<i>L. lucens</i>	18	16	18	19	18	—	—	—	—	—	—	—	—	—	—
<i>L. pullitarsis</i>	—	—	—	2	—	19	19	13	16	16	—	—	—	—	—
<i>L. rufitarsis</i>	2	1	—	1	—	—	—	—	—	—	19	19	20	17	17
<i>Haplegis spec. A</i>	—	1	—	2	—	—	3	1	—	—	—	—	—	—	—
<i>Haplegis spec. B</i>	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—

b. Egg-laying behaviour

The egg-laying behaviour of *Lipara lucens* has been investigated extensively (Mook, 1967). The species is autogenic: it does not need food to lay eggs. At emergence the ovaries contain almost mature eggs, and egg-laying can start two or three days later. The number of eggs in the ovaries of *L. lucens* lies between 64 and 96, with a mean of 84 (data from 40 Dutch specimens). However, egg production is not limited to this

number. In laboratory experiments the flies were often observed laying eggs in two or three periods of one or two days, each period separated by two or three days in which no eggs were laid. The number of eggs laid during the first of these periods corresponded to the number of mature eggs in the ovaries at emergence. In the later periods a smaller number of eggs was laid, so that the total production of eggs often attained twice the number of eggs originally present in the ovaries. Under favourable circumstances (the flies were provided daily with fresh drinking water and pieces of fresh reed shoot of the preferred diameter; light and a temperature of 20° C were maintained for 7 hours each day) the number of eggs laid was between 0 and 199, with a mean of 133.6 (median 147).

Comparable data for the other species are lacking. At emergence they too have almost mature eggs in the ovaries. For *L. pullitarsis* the number of eggs in the ovaries lies between 98 and 157 in 20 Dutch specimens and for *L. rufitarsis* between 54 to 83 in 17 Dutch specimens. No data are available for *L. similis*.

Lipara lucens lays its eggs during the warmest hours of the day. The female flies to a reed shoot and walks on it, first upward. After reaching the top of the shoot it often turns and walks down again. During this walking the ovipositor may be slightly extended, but does not touch the shoot. After a while the female begins to walk on a more restricted part of the shoot, a few centimeters' distance. By this time the ovipositor is fully extended and its tip now and then touches the surface of the shoot. The fly then pauses for about 60 seconds with its head pointing upward, after which the egg emerges from the tip of the ovipositor and is pressed against the surface of the shoot. After the egg has been laid the female walks upwards and usually flies away to another shoot.

The eggs are usually laid on the stem, sometimes but not always on or under the hairy ligules, but in an outdoor cage an appreciable proportion of the eggs was found on the reed blades. The flies show a marked preference for ovipositing on shoots of a certain diameter; nonpreferred shoots are generally deserted during the walking stage of this ovipositional behaviour. Because this preference influences the habitat relationships, it will be treated in the next section.

5. ECOLOGY

a. Habitat relations

In the literature it is often stated that the galls of *Lipara lucens* are most numerous in reed stands located in dry places (Wagner, 1907; Docters van Leeuwen, 1957; Ruppolt, 1957), but this does not necessarily imply that the water level itself influences the species. Together with the water level, characteristics of the vegetation vary considerably. The number of shoots per square metre, for instance, tends to be higher in drier places (but is lower again where the soil becomes very dry). The dimensions of the reed shoots are also influenced by the water level, the shoots being shorter and thinner in dry than in wet places.

A partial regression analysis of samples of three different vegetations showed that the variation in gall density is not primarily due to variations in water level or shoot density, but to variations in the dimensions of the shoots. In this analysis and in the subsequent experimental work the basal diameter of the shoots was chosen as the most characteristic shoot dimension, because this is the most constant measure throughout the year and is not influenced by gall formation. The basal diameter does not alter during

the growing season and when the reed dries in the autumn it diminishes only by about 10 per cent.

Experimental work in the field and in the laboratory showed that the diameter of the reed shoots plays an important role in the biology of *Lipara lucens*, in some cases directly affecting the behaviour of the fly or its parasites, in other cases correlated only with the real operating factor. The correlation of life functions of *Lipara lucens* with the diameter of the reed shoots has been treated elsewhere (Mook, 1967); only a short survey will be given here.

The female flies lay their eggs preferentially on shoots with a width of 4 and 5 mm at the base. In Fig. 19a oviposition is expressed as the mean number of eggs per shoot, thus eliminating the influence of the number of shoots available in each class. Waitzbauer (1969) found a distribution of eggs in the field with an optimum on shoots with a diameter of 4–4.5 mm, but he did not take into account the distribution of shoot

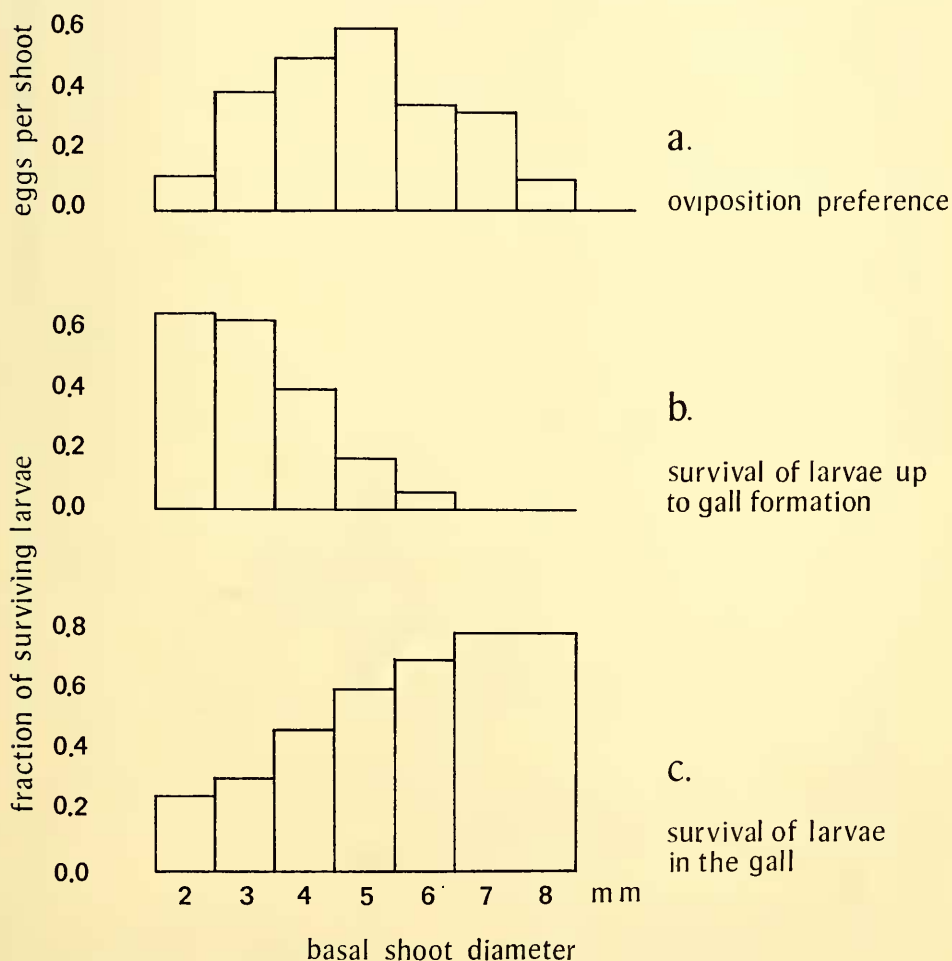
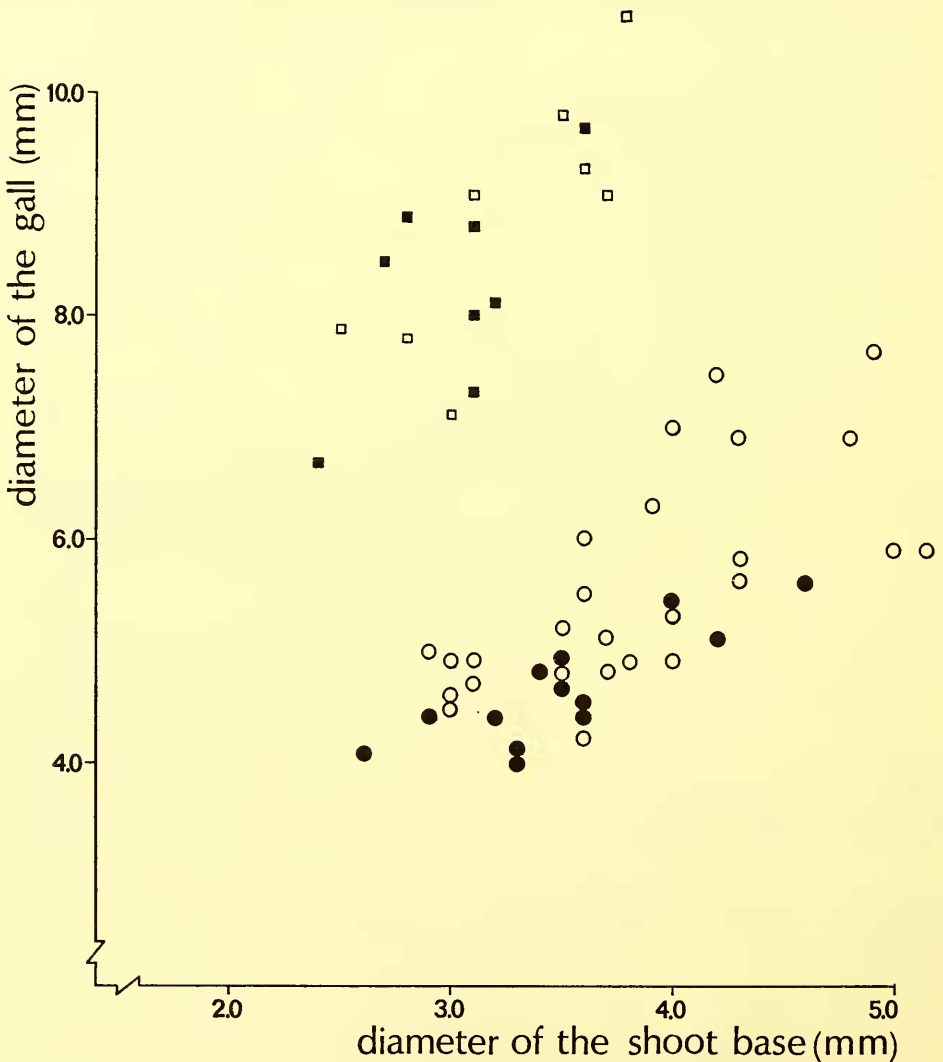


Fig. 19. *Lipara lucens* Meig. Correlation of oviposition and survival of larvae with diameter of reed shoots

diameter in the vegetation. He states that Mook (1967) found a preference for shoots with a diameter of 2.5—2.9 mm, but this is derived from a laboratory experiment in which the diameter of the shoot top was used. This value corresponds to a basal diameter of about 4 mm.

Once a shoot has received an egg, the probability that a gall will be formed is also correlated with shoot width (Fig. 19b). It is in the shoots with a diameter of about 2 and 3 mm that the young larvae have the greatest chance to induce a gall and thus the greatest chance to survive. The differences in survival of larvae in the gall (fig. 19c) are due to a heavier parasitism by *Stenomalina* and more predation by birds on the thinner shoots.

Multiplication of the estimates of oviposition preference and survival up to gall



formation in one diameter class gives the probability that a shoot in that class will develop a gall. This appears to be highest on shoots with a diameter of 3 and 4 mm, and this estimate agrees with the fractions of galled shoots in each class found in the field. In the field a low number of galls is also found on shoots with a diameter of 7 or 8 mm and sometimes even more, so that the chance of gall formation cannot be zero as in the experiment of Fig. 19b. The experiments were of course, all carried out with a limited number of shoots, so that chance variation can be important.

This analytical approach explains why the highest density of galls can be found in

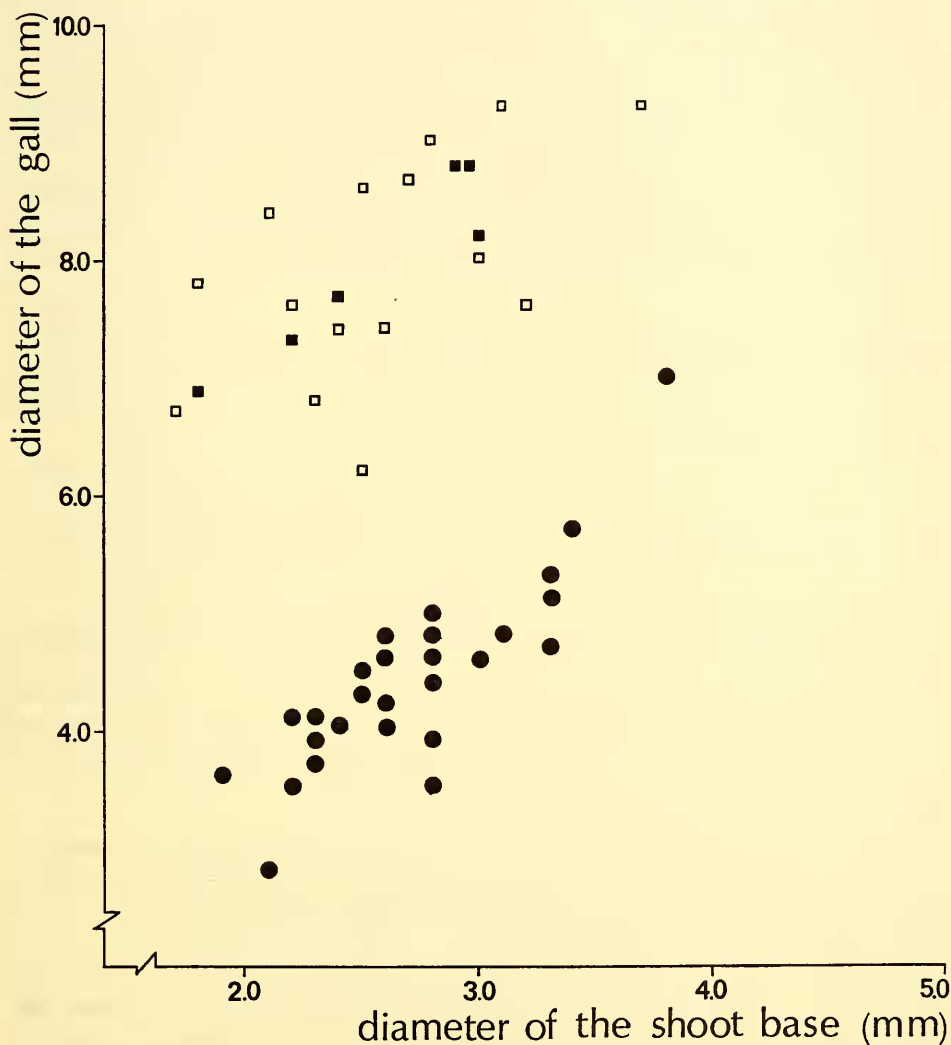


Fig. 20—21. Correlation between basal diameter of reed shoot and diameter of gall occurring on that shoot, for different types of galls: lignified galls containing larvae of *L. lucens* (□) and *L. rufitarsis* (■), and soft walled galls with larvae of *L. rufitarsis* (●) and *L. pullitarsis* (○). Galls collected in Voorsterbos (Fig. 20: parcel T 35, Fig. 21 parcel S 18), N.O. Polder, The Netherlands 11-1-1963

places where a large proportion of the reed shoots have a width of about 3 or 4 mm.

It may be concluded that most galls of *Lipara lucens* are found in reed with sub-optimal growth, but not in reed with the worst growth. Although the water level has no direct influence, it can be said that reed with suboptimal growth is found mainly in dry places. On the basis of experience with a wide variety of reed vegetations in the Netherlands it can be said that there is no predilection for reed growing in extensive vegetations, as compared to reed in smaller patches, for instance in small bogs, along ditches, etc.

Lipara rufitarsis and especially *L. pullitarsis* are not as abundant in the Netherlands as *L. lucens*. Only superficial observations on their habitat are available, but comparison with *L. lucens* is possible. In reed vegetations where two or three species are present the galls of *L. rufitarsis* and *L. lucens* occur on shoots with about the same diameter, but the shoots with galls of *L. pullitarsis* on the average have a larger diameter. This can be seen, for instance, in Fig. 20, but has also been found in many other vegetations.

Galls of *L. rufitarsis* are sometimes present in low numbers in closed reed vegetations on dry soil, together with *L. lucens*, but occur much more abundantly in smaller reed vegetations in dry places at the edge of woods or along roadsides or other somewhat shaded places. In such places they are often more numerous than *L. lucens*.

Galls of *L. pullitarsis* were found in small reed stands with a low shoot density (often located between trees or bushes) in wetter, marshier places than those where *L. rufitarsis* has its optimum. In the Netherlands no galls of *pullitarsis* were found in large closed reed vegetations. This shows clearly that shoot dimension is not the only important factor determining the habitat of *Lipara* species.

In places where *L. rufitarsis* and *L. lucens* occur together, the larvae of the former species are sometimes found in galls that are indistinguishable from those of the latter species. This peculiar phenomenon has already been reported by Ruppolt (1957), but he did not describe *L. rufitarsis* in its typical galls. The thin galls with larvae he describes under the name of *L. rufitarsis*, undoubtedly refer to *L. pullitarsis*.

The two types of galls in which *rufitarsis* is found are quite different. That no intermediate forms occur is evident, e.g. in Figs. 20 and 21, showing two distinct groups of dots. The upper group corresponds with the wide galls with thickened internodes and lignified walls, the lower group, with narrow galls of which the internodes are not thickened. For both types of gall there is a strong positive correlation between shoot and gall width illustrating that the diameter and other dimensions of a gall are significant only in relation to shoot diameter.

Analysis of the morphology of the larvae and adults and also of the acoustical signals of the male flies, proved that the same species (*rufitarsis*) occurs in both types of gall. A few galls of the *lucens* type have also been found in which only a *pullitarsis* larva was present (above the growing point).

It is difficult to believe that one species can induce different galls on the same food plant. We know that when a shoot is infected by more than one egg, never more than one larva will survive. When these eggs are of different species, it cannot be said beforehand which species will survive. In the case of multiple infection by *lucens* and by one of the smaller species, if the *lucens* larva dies the result will be a typical *lucens* gall with a surviving *rufitarsis* or *pullitarsis* larva. This only holds, however, if the *lucens* larva does not die before the gall reaches maturity, since otherwise we would find a gall of intermediate size. We know that gall growth stops when a *lucens* larva dies before

gall maturation, because we find rudiments of galls above which the shoot has resumed normal growth. This does not imply, however, that *lucens* will always succumb to the smaller species. Without extensive breeding experiments, it will be impossible to judge the outcome of interspecific competition.

b. Parasites

Hymenopterous parasites belonging to four families attack the different species of *Lipara*. We have not tried to give a comprehensive list of these parasites. Only the common species with which we are acquainted will be treated here, because the records of occasional parasites are difficult to check. It is important to rear from material found in opened galls, to be sure that the parasites originate from *Lipara* larvae and not from the numerous species of inquiline that are also present in the galls.

The occurrence of parasites differs widely between the types of galls. Table II shows the numbers of hosts and parasites found in galls collected in a number of localities in the central and eastern part of the Netherlands. The *lucens* galls included here originate exclusively from places where this species occurred together with one or both of the other fly species. More figures on parasitism of *L. lucens* have been given elsewhere (Mook, 1967).

The findings of Table II cannot be generalized for other regions. The relative importance of the parasites in different regions is indicated below under the different species.

Table II. Distribution of host and parasite larvae over 3 types of galls collected in various places in the Netherlands

Species of larvae	Type of gall		
	<i>lucens</i>	<i>rufitarsis</i>	<i>pullitarsis</i>
<i>Lipara lucens</i>	191	—	—
<i>Lipara rufitarsis</i>	31	240	—
<i>Lipara pullitarsis</i>	9	—	119
<i>Polemon liparae</i>	83	—	—
<i>Stenomalina liparae</i>	58	8	13
<i>Scambus phragmitidis</i>	1	113	4
Total	373	361	136

Ichneumonidae: From Table II it is apparent that *Scambus phragmitidis* Perk. is primarily a parasite of *L. rufitarsis*. Waitzbauer (1969) reared one specimen from *lucens* in Austria (Neusiedler See). In the Netherlands we have found a few in galls of *lucens*, but always in places where *rufitarsis* also occurred in *lucens* galls. This parasite was erroneously named *Pimpla arundinator* F. var. *similis* Bridgm. in Mook (1967). The new identification was made by Mr. K. W. R. Zwart, Wageningen, who compared specimens with paratypes from the British Museum (Natural History), London.

The distribution is difficult to assess. Pokorný did not find *Scambus* in Czechoslovakia. Other species of the same genus have been mentioned in the literature: Giraud (1863) reared *Scambus* (= *Pimpla*) *arundinator* F. as a parasite of *L. rufitarsis* or *L. pullitarsis* in Austria, while Wagner (1907) in Germany (Hamburg) and Blair (1944b) in England mention *Scambus* (= *Pimpla*) *detritus* Holmgr. from galls of *L. lucens*.

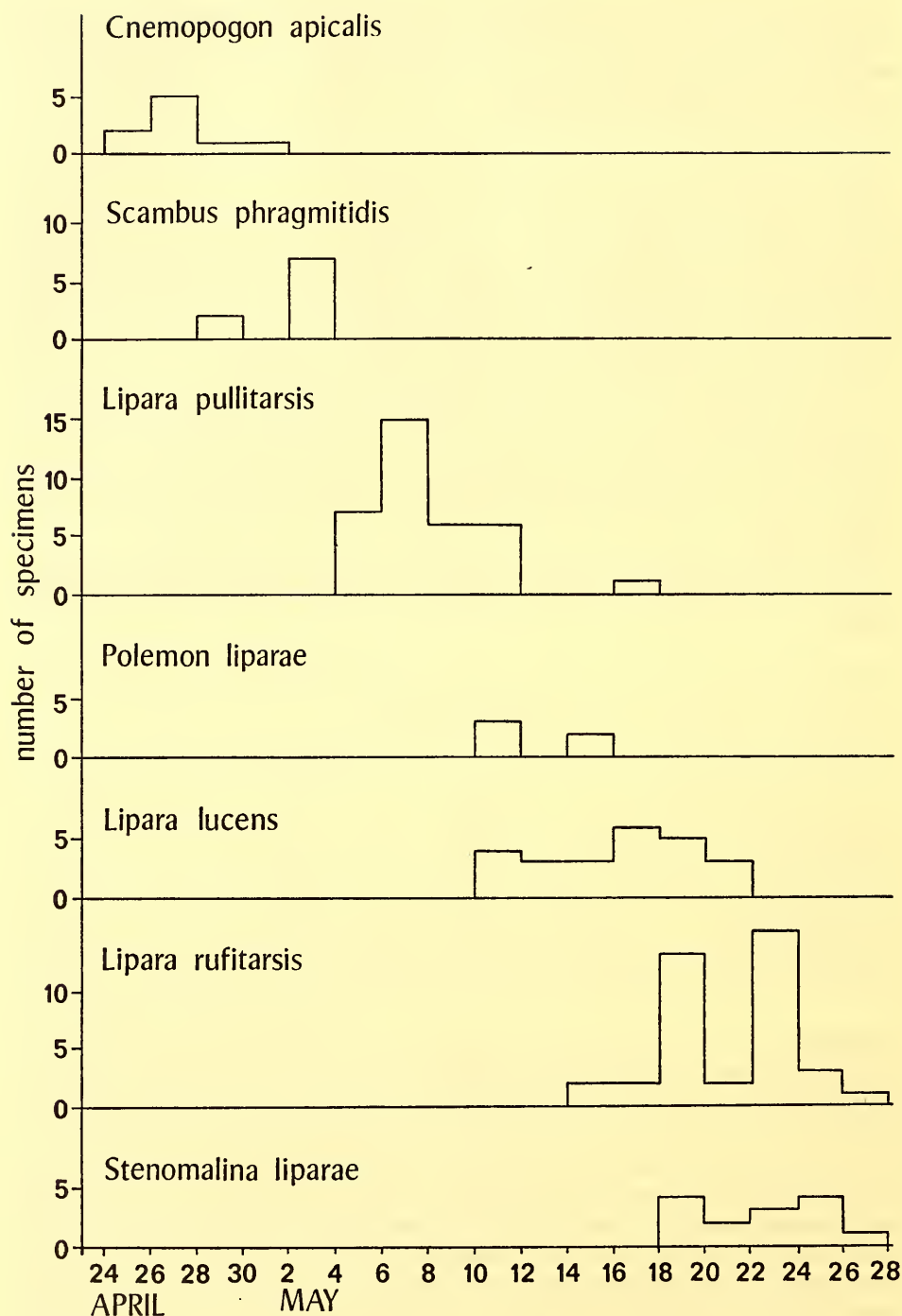


Fig. 22. Emergence in the laboratory of adult flies, predators and parasites from galls collected in N.O. Polder and near Dalfsen, The Netherlands, 20-IV-1962

Of the life history of *Scambus phragmitidis* nothing more is known than that it emerges early in the season (see Fig. 22), long before *L. rufitarsis*. The oviposition behaviour has not been studied.

Braconidae: Two species of *Polemon* have been described: *P. liparae* Gir. and *P. melas* Gir. In the Netherlands *P. liparae* is primarily a parasite of *L. lucens*. In Austria (Waitzbauer, 1969) and Czechoslovakia (Pokorný) it is by far the most important parasite of *L. lucens*, while in Hungary it was the only parasite found in this host (Erdős, 1961). Giraud (1863) mentions this species as the only parasite of *Lipara similis*.

Polemon melas is the most important parasite of *L. rufitarsis* in Czechoslovakia (Pokorný). Giraud (1863) found it in Austria. It was reared occasionally in the Netherlands (Reynvaan and Docters van Leeuwen, 1906).

Polemon liparae emerges from the tip of the gall just as its host and at the same time as *L. lucens*. It oviposits in the eggs of *lucens* (Mook, 1961). Larvae of *lucens* parasitized by *Polemon* form a puparium in September instead of in the spring, as they normally do. A puparium containing a parasite can be distinguished from the normal by being reddish-brown and slightly more slender. Varley and Butler (1933, see also Askew, 1971) have suggested that the premature pupation might be caused by wounding by the ovipositing parasite. This is improbable because of the long time lying between infection and pupation.

Pteromalidae. *Stenomalina* (= *Pteromalus*) *liparae* Gir. was found in the Netherlands in galls of *lucens*, *rufitarsis* and *pullitarsis* (see Table II), but most commonly in *lucens*. In England (Blair, 1932) and western Germany (Hamburg, Wagner, 1907) it is the most common parasite of *lucens*. In Czechoslovakia it is not common (Pokorný); it was not found in eastern Austria (Neusiedler See) by Waitzbauer (1969) and in Hungary by Erdős (1961). Giraud (1863) has described it from material collected near Vienna and indicates that it was rather common there.

The adults of *Stenomalina liparae* leave the gall by biting a small round hole in the leaf sheaths just above the gall chamber. They begin to emerge about 8—10 days later than *L. lucens*. They parasitize the young larvae living above the growing point, by boring through the leaf sheaths. In view of the circumstance that the first larvae of *lucens* arrive above the growing point in the period that *Stenomalina* starts to emerge and that this species does not need much time between emergence and oviposition, it seems that its life cycle is primarily synchronized to that of *L. lucens*.

Eulophidae. *Tetrastichus legionarius* Gir. is mentioned as a parasite of *L. lucens* in Czechoslovakia (Pokorný), Austria (Giraud, 1863), and the DDR (Greifswald, Ruppolt, 1957), but seems nowhere to be common. Erdős (1961) mentions the species from Hungary as a parasite of *Haplegis flavitarsis* Mg., a small chloropid fly that is an inquiline in *Lipara* galls. In the Netherlands *T. legionarius* is rare in *lucens*. We have found only recently two parasitized puparia, after having opened more than 10,000 galls from various places, although mainly from the eastern part of the country. Mr. M. J. Gijswijt ('s-Graveland), who kindly identified our specimen, informed us that the species has also been reared from *lucens* galls from three localities in the central and southern parts of the Netherlands. It is a gregarious parasite: our puparia contained 25 and 28 larvae respectively.

c. Predators

Birds attack the galls of *L. rufitarsis* in particular and also the smaller galls of *L. lucens* occurring on narrow shoots and, less often, the galls of *L. pullitarsis*. The intensity of this predation differs widely between winters. Blue Tits (*Parus caeruleus* L.) are known to predate in winter on all kinds of insects in reed stems (Tischler, 1943). Actual observations of predating tits are scarce, but they are at least known to be able to open the galls (Mook, 1967). Kramer (1917) observed a Great Spotted Woodpecker (*Dryobates major* L.), opening a gall of *L. lucens*.

Puparia of *Cnemopogon apicalis* Wiedemann (Diptera, Scatophagidae) are found in the winter in small numbers between the top blades of all three types of galls. The host larvae are always absent, presumably having been consumed by the *Cnemopogon* larvae (Wagner, 1907; Theowald, 1961).

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